Climate change, species range shifts and uncertainty – a new era of conservation planning

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ACADEMIC DISSERTATION

To be presented for public examination with the permission of the Faculty of Biological and Environmental Sciences of the University of Helsinki in Auditorium 2, Info Centre Korona (Viikinkaari 11), on June 1st 2012 at 12 o'clock noon.

HELSINKI 2012

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ISBN 978-952-10-8022-7 (paperback)
ISBN 978-952-10-8023-4 (PDF)
http://ethesis.helsinki.fi

Yliopistopaino
Helsinki 2012

"I love fools experiments. I am always making them."

— Charles R. Darwin

Contents

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I **Kujala, H.**, Vepsäläinen, V., Zuckerberg, B. & Brommer, J. Range margin shifts of birds revisited — the role of spatiotemporally varying survey effort. – *To be resubmitted to Global Change Biology*.

II **Kujala, H.**, Lehikoinen, A., Valkama, J., Pironon, S. & Thuiller, W. Feeling the heat: Boreal breeding birds follow modelled expectations under climate change. *Manuscript*

III **Kujala, H.**, Araújo, M. B., Thuiller, W. & Cabeza, M. (2011) Misleading results from conventional gap analysis – Messages from the warming north. *Biological Conservation*. 144(10): 2450-2458.

IV **Kujala, H.***, Araújo, M. B, Moilanen, A. & Cabeza, M.*. Conservation planning with uncertain climate change projections. – *Submitted manuscript.*

* these authors have contributed equally

V **Kujala, H.**, Burgman, M.A. & Moilanen, A. Treatment of uncertainty in conservation under climate change. – *In revision in Conservation Letters.*

Table of contributions

	I	II	III	IV	V
Original idea	HK, VV	HK	HK, MC	AM, MC	AM, HK
Study design	HK, VV, JB	HK, WT	HK, MC	AM, MC, HK	HK, AM, MB
Analyses	HK, VV, JB, BZ	HK, AL	HK	HK	HK
Empirical data	-	AL, JV, WT, SP	WT, MBA	MBA	-
Manuscript preparation	HK, JB, BZ, VV	HK, WT, AL	HK, MC, MBA	MC, HK, AM, MBA	HK, AM, MB

HK = Heini Kujala, MC = Mar Cabeza, AM = Atte Moilanen, MBA = Miguel Bastos Araújo, WT = Wilfried Thuiller, VV = Ville Vepsäläinen, JB = Jon E. Brommer, AL = Aleksi Lehikoinen, JV = Jari Valkama, SP = Samuel Pironon, MB = Mark A. Burgman, BZ = Benjamin Zuckerberg

ABSTRACT

All species are adapted to certain climatic conditions, outside of which they cannot survive. Changes in the climatic environment therefore force species to either adapt to the new conditions or move to areas where suitable conditions are still present in order to avoid extinction. Several studies have shown that species from various taxa are currently moving their ranges polewards and to higher elevations to keep up with shifting climate regimes. However, species differ widely in their dispersal abilities. In addition, natural landscapes are becoming increasingly human-dominated, further hindering dispersal by decreasing permeability. Anthropogenic climate change is therefore expected to become one of the major drivers of species extinctions by the end of the 21st century.

Species range shifts are problematic in conservation planning, because dynamic biodiversity patterns hamper our ability to identify priority areas for protection. Because protected area networks are geographically fixed, climate change may also drive species out of reserves, foiling past conservation efforts. In this thesis the different risks and opportunities of conducting conservation planning under climate change are investigated. This research focuses on the uncertainties that arise from working with unknown future events, technical challenges of observing and predicting species range shifts, and using (or ignoring) information about future impacts in conservation planning.

The major findings of this thesis are that climate change is already rapidly reshaping species distributions in Finland and that ignoring future dynamics can lead to misguided and potentially inefficient conservation decisions. The results presented here show that modelling future impacts using so-called niche modelling techniques, despite their inherent uncertainties, can provide useful information about how species distributions and conservation statuses will be affected by climate change. For example previously created models for Finnish breeding birds predicted well recently observed changes in species distribution sizes. More importantly, the observed changes seem to match best with predictions that follow the most extreme climate change scenario. A key factor for successfully measuring and predicting climate change impacts are good monitoring data, the role of which should be more widely acknowledged by decision-makers.

Uncertainty in climate change research is pervasive and cannot ever be entirely eliminated. This work offers tools to assist in both spatial prioritization and decision making when scarce conservation resources need to be allocated under uncertain future conditions. The findings of this thesis strongly encourage using proactive approaches that account for future impacts. The results also suggests that while striving to reduce epistemic uncertainty is important in climate change and conservation research, other sources of uncertainty such as socio-political factors or volitional human behaviour might constitute far larger determinants of successful conservation actions, and therefore merit stronger focus in research.

TIIVISTELMÄ

Kaikki eliölajit ovat sopeutuneet niille ominaisiin ilmasto-olosuhteisiin, jotka määrittävät lajin esiintymisalueen. Kun ilmasto-olosuhteet muuttuvat, lajin täytyy sukupuuton välttääkseen joko evolutiivisesti sopeutua uusiin ilmasto-olosuhteisiin tai siirtyä alueille, missä olosuhteet ovat sille edelleen suotuisat. Useat tutkimukset ovat osoittaneet, että viimeaikaisen ilmaston lämpenemisen seurauksena lajien levinneisyysalueet ovat alkaneet siirtyä kohti napa-alueita ja vuoristoisia ylänköjä, mikä viittaa siihen, että lajit pyrkivät seuraamaan niille ominaisia ilmasto-olostuhteita. Lajien levinneisyysalueiden siirtymisnopeus vaihtelee kuitenkin suuresti, ja levittäytymistä uusille alueille voi merkittävästi hidastaa ihmistoiminnan aiheuttama luonnonympäristöjen pirstaloituminen ja häviäminen. Ilmastonmuutoksesta onkin ennustettu lähitulevaisuudessa tulevan merkittävä uhkatekijä luonnon monimuotoisuuden säilymiselle.

Tässä väitöskirjassa on tutkittu ilmastonmuutoksen luomia haasteita ja mahdollisuuksia suojelusuunnittelulle. Lajien levinneisyysalueiden nopea muuttuminen vaikeuttaa suojelun kannalta tärkeiden alueiden tunnistamista. Ilmastonmuutos voi lisäksi heikentää jo saavutettuja suojelutavoitteita, sillä ilmaston muuttuessa jo suojellut lajit voivat joutua siirtymään suojelualueiden ulkopuolelle. Tässä väitöskirjassa tarkastellaan erityisesti levinneisyysalueiden muutosten mittaamiseen ja ennustamiseen liittyviä epävarmuuksia, sekä sitä miten tätä tietoa tulisi hyödyntää suojelusuunnittelussa.

Kirjassa esitetyt tutkimustulokset osoittavat, että lajien levinneisyysalueet ovat nopeasti muuttumassa myös Suomessa, ja että onnistuneet ja kustannustehokkaat suojelutoimet edellyttävät ilmastonmuutoksen vaikutusten ennakoivaa huomioimista. Epävarmuuksista huolimatta, levinneisyysalueiden siirtymistä ennustavat mallit tarjoavat tärkeää ja käyttökelpoista tietoa ilmastonmuutoksen vaikutuksista lajeihin ja niiden suojeluun. Tässä väitöskirjassa esitetyt tulokset osoittavat mm. että Suomessa pesiville lintulajeille aikaisemmin tehdyt mallinnukset ovat onnistuneet ennustamaan hyvin viimeaikaisia levinneisyysalueiden muutoksia. Lisäksi tulokset osoittavat, että havaitut muutokset vastaavat parhaiten kaikkein voimakkaimman ilmastonmuutoksen ennusteita. Muutosten havainnoimisen ja ennustamisen kannalta on kuitenkin ensisijaisen tärkeää panostaa nykyistä enemmän lajistoseurantoihin ja tästä kerättävien aineistojen laatuun. Tämä vaatii ensikädessä seurantaohjelmien resurssien parantamista.

Ilmastonmuutos ja sen vaikutukset ovat haastavia tutkimuskohteita, eikä niihin liittyvää epävarmuutta voida koskaan täysin poistaa. Tämä väitöskirja tarjoaa kuitenkin työkaluja, joiden avulla luonnonsuojelua voidaan suunnitella tulevan ilmastonmuutoksen epävarmuuksia huomioiden ja niitä ennakoiden. Kirjassa esitetyt tulokset osoittavat myös, että tietopohjaisten epävarmuuksien vähentämisen lisäksi tulisi kiinnittää nykyistä enemmän huomiota myös muihin epävarmuuksien lähteisiin. Suojelutoimien onnistumiseen voi tieteellisten seikkojen sijaan vaikuttaa huomattavasti enemmän sosio-poliittiset tekijät sekä sidosryhmien käytösmallit tai arvomaailmat.

SUMMARY

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1. INTRODUCTION

1.1. ANTHROPOGENIC CLIMATE CHANGE AND ITS IMPACTS ON BIODIVERSITY

During the past 150 years, average land surface temperatures have increased globally by 0.8°C (IPCC 2007a). There is substantial evidence that the current global changes in average temperature and rainfall cannot be entirely explained by natural variation but are caused by anthropogenic actions, such as increases in greenhouse gas (GHG) emissions and conversion of natural land areas (Stott 2003; Matthews et al. 2004; IPCC 2007a; Rosenzweig et al. 2008). According to modelled projections, the global mean temperatures are expected to increase 1.1–6.4°C by the end of 21st century, depending on the development of GHG emissions and actions of human society (IPCC 2000; 2007a, Box 1).

Changes in climate have complex direct and indirect impacts on species and communities. As the environmental conditions change, species are forced to either adapt to the new conditions or move to areas where suitable conditions are still present to avoid extinction (Parmesan 2006). Some species have shown considerable adaptive plasticity (Nylin and Gotthard 1998; Price et al. 2003; Réale et al. 2003), which allows them to adjust to new conditions by changing their behaviour (Tebbich et al. 2001), phenology (i.e. timing of yearly events, such as migration of birds or flowering of plants) (Menzel and Dose 2005; Charmantier et al. 2008) or certain biochemical or morphological characters (Post et al. 1999; Przybylo et al. 2000). However, reports of true evolutionary processes where a species has become more adapted to the new conditions through changes in its genetic heritage are to date rare (Gienapp et al. 2008, but see Berthold et al. 1992; Levitan 2003; Karell et al. 2011 for examples of evolutionary responses). Furthermore, although studies of adaptive responses are accumulating, it is speculated that the speed of climate change might be too fast for evolutionary processes to take place (Bürger and Lynch 1995; Gomulkiewicz and Holt 1995; Donner et al. 2005). It is therefore expected that adaptation is a viable strategy only to a small fraction of species and that the majority will be forced to shift their distributions in order to survive the forthcoming changes (Parmesan 2006, Fig. 1). This view is also supported by evidence from paleoecological records, such as fossils and historical pollen data, which implies that species have typically responded to past climate changes with rapid distribution shifts rather than remaining stationary and adapting to new conditions (Huntley 1991; Coope and Wilkins 1994). Under general warming trends species' *climate-envelopes*, which define the climatic conditions within which species can persist, become shifted towards poles and to higher altitudes (Walther et al. 2005; Loarie et al. 2009). Species' ability to track their moving climate envelope depends on several factors such as dispersal capability, fecundity, resource and habitat needs etc. (Warren et al. 2001). Changes in species distributions further affect community structures, re-ordering assemblages and creating entirely new community compositions where newly established species interactions can have unforeseeable impacts (Graham and Grimm 1990; Pounds et al. 1999; Harley 2011).

A group of major concern is species that currently inhabit polar regions and mountainous areas, as they are in risk of losing their entire suitable climatic space and are therefore most likely to face extinction (Sala et al. 2000; Nogués-Bravo et al. 2007). But also other species might face considerable challenges in tracking their climate envelopes (Devictor et al. 2008). An accumulating amount of studies imply that climate change will become one of the major threats to biodiversity in the coming century (Sala et al. 2000; Thomas et al. 2004; Millennium Ecosystem Assessment 2005; Jetz et al. 2007). Species

BOX 1. SRES emission scenarios

To understand how human actions might influence the development of future climate change, the Intergovernmental Panel of Climate Change (IPCC) has produced a set of scenarios to describe potential future development of greenhouse gas (GHG) emissions by the end of 21st century. In 2000 IPCC published the Special Report on Emission Scenarios (SRES, Nacinovenic & Swart 2000) which lists 40 different scenarios that are grouped under four different storylines, also called scenario families (A1, A2, B1 and B2). These main storylines diverge in terms of their key assumptions about human demography changes, global socio-economical dynamics and technological developments. Scenarios from each of the scenario family assume distinctly different directions for future development, and their differences become increasingly irreversible with time. Together they describe divergent futures that are believed to capture most of the unknown development options. To simplify research steps and reporting of results in climate change research, scenarios in each family are typically averaged to one scenario which then represents the entire family. Below is a short description of each of the main families, adopted from Nacinovenic & Swart (2000) and IPCC Summary for Policymakers (2007). All estimated increases in average temperatures are calculated by the end of 21st century. When the SRES scenarios were released, IPCC stated that all 40 different scenarios were assumed to be equally plausible and should be treated as such also in research. However, observations from the increased atmospheric CO_2 levels imply that during the first decade after the publication of SRES scenarios, anthropogenic GHG emissions have promptly followed the most extreme and fossil intensive scenario option A1FI (Le Quéré et al. 2009).

A1 This storyline describes a future world of very rapid economic growth, global population that peaks in mid-century and declines thereafter, and the rapid introduction of new and more efficient technologies. Major underlying themes are convergence among regions, capacity building, and increased cultural and social interactions, with a substantial reduction in regional differences in per capita income. The A1 scenario family differs from the other families in the sense that it develops into three groups that describe alternative directions of technological change in the energy system. The three A1 groups are distinguished by their technological emphasis: fossil intensive (A1FI), non-fossil energy sources (A1T), or a balance across all sources (A1B). Out of all scenario families and groups A1FI has the highest emissions throughout the 21st century, leading to an estimated increase in average temperature of 4.0 °C (best estimate, range 2.4–6.4°C) by the year 2100. Similar estimates for A1B and A1T are 2.8°C (1.7–4.4°C) and 2.4°C (1.4–3.8°C), respectively.

A2 The A2 storyline describes a very heterogeneous world where the underlying theme is self-reliance and preservation of local identities. Fertility patterns across regions converge very slowly, which results in continuously increasing global population. Economic development is primarily regionally oriented, and per capita economic growth and technological changes are more fragmented and slower than in other storylines. Emissions in A2 storyline increase rapidly after midpoint of 21st century, leading to an increase of 3.4°C (best estimate, range 2.0–5.4°C).

B1 The B1 storyline describes a convergent world with the same global population that peaks in midcentury and declines thereafter, as in the A1 storyline, but with rapid changes in economic structures toward a service and information economy, with reductions in material intensity and the introduction of clean and resource-efficient technologies. The emphasis is on global solutions to economic, social, and environmental sustainability, including improved equity, but without additional climate initiatives. Emissions are among the smallest in B1 storyline, yet potentially larger than in storyline A1T. Best estimate 1.8°C, range 1.1–2.9°C.

B2 This storyline is often called the midrange option of all SRES scenarios. The B2 storyline describes a world in which the emphasis is on local solutions to economic, social, and environmental sustainability. It is a world with continuously increasing global population at a rate lower than A2, intermediate levels of economic development, and less rapid and more diverse technological change than in the B1 and A1 storylines. While the scenario is also oriented toward environmental protection and social equity, it focuses on local and regional levels. Best estimate 2.4°C, range 1.4–3.8°C.

Source: Nacinovenic & Swart (2000) and IPCC (2007b)

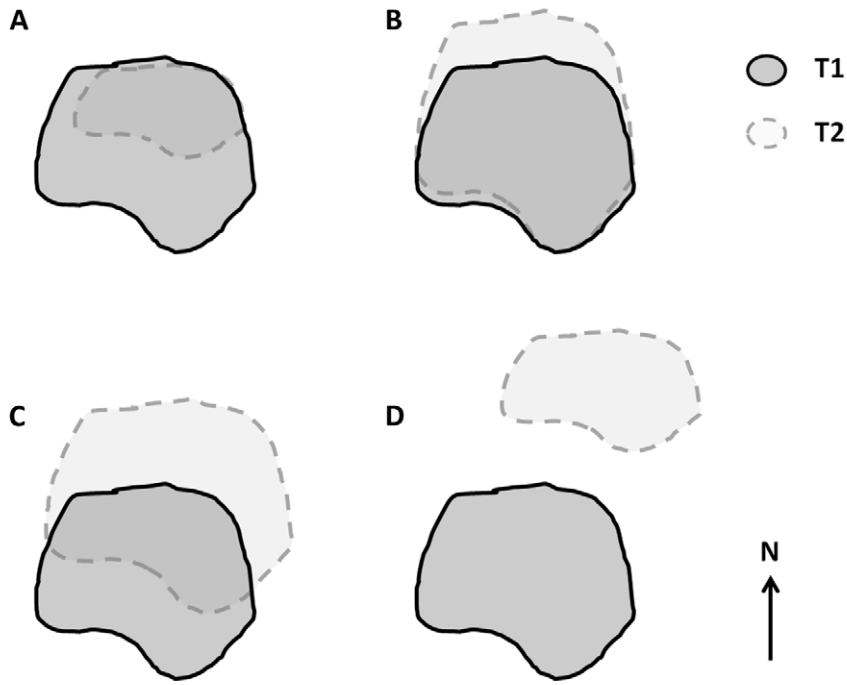

Figure 1 | Schematic illustration of potential dynamics in species' climate envelopes on the Northern Hemisphere under climate change. At time 1 (T1) species' climate envelope is marked with dark grey, and at time 2 (T2) with light grey. Panel **a.** shows a typical contraction in the climate envelope where the warm edge shifts along environmental gradient but cold edge does not show significant changes, leading to a decreased total area. This is the most typical scenario for species inhabiting polar regions and mountain tops, however, it can be a likely scenario for any other species. Panel **b.** illustrates an expansion where the cold edge shifts and warm edge does not show significant changes. Note that expansions and contractions can take place anywhere along species' climate envelope – hence, also species' cold edge can contract and warm edge expand (not illustrated here). Panels **c.** and **d.** show two types of shifts where during T1 and T2 the climate envelopes of species are **c.** overlapping, allowing species to persist in areas that remain suitable during both time periods, or **d.** non-overlapping, in which case species is forced to migrate between T1 and T2 in order to persist. On Southern Hemisphere the poleward direction would result in climate envelopes moving southwards. Overall, species' climate envelope changes are simultaneously characterized by i) the amount of overlap between T1 and T2, ii) direction of shift, and iii) changes in the size of climate envelope between T1 and T2.

distribution shifts have already been reported (Walther et al. 2005; Hickling et al. 2006; Devictor et al. 2008; Chen et al. 2011) and there are speculations that recent changes in climate have already resulted in several extinctions of species (McLaughlin et al. 2002; Pounds et al. 2006). As climate is expected to change with accelerating pace in the future (IPCC 2007a; Loarie et al. 2009), the majority of species will be forced to shift their distributions with unparalleled rates. Depending on the severity and speed of forthcoming changes as well as species' abilities to follow their shifting climate envelopes, it has been estimated that roughly 10 to 50% of all known species might face global extinction due to climate change during the 21st century (Bellard et al. 2012 and references therein).

The challenges posed by climate change are further amplified by today's high levels of habitat fragmentation and habitat loss (Travis 2003; Opdam and Wascher 2004; Jetz et al. 2007) as more than 30% of all land surfaces have been partly or entirely converted by human actions (Mock 2001; Millennium Ecosystem Assessment 2005). Decrease in the amount of suitable habitat leading to decreases in population sizes is a threat to species *per se*, but in addition it makes species more vulnerable to climate change. This is because small populations are

less capable to adapt and respond to environmental changes and are more likely to be detrimentally affected by stochastic events, such as droughts or floods (Lawton 1993; Hanski 1998; Gaston 2003). Furthermore, human dominated landscapes can act as dispersal barriers significantly hindering species' abilities to disperse to new areas and establish new viable populations (Travis 2003; Opdam and Wascher 2004).

1.2. SYSTEMATIC CONSERVATION PLANNING IN A CHANGING WORLD

Systematic conservation planning is a discipline that has emerged over the past few decades to guide efficient allocation of scarce resources in biodiversity protection (Soulé 1985; Noss 1990; Margules and Pressey 2000). In a time of biodiversity crisis, when species are going extinct alarmingly faster than expected on the basis of natural background rates (Smith et al. 1993; Pimm et al. 1995; Millennium Ecosystem Assessment 2005; Pereira et al. 2010), methods to identify conservation needs and to implement actions in a cost-efficient and effective manner are urgently needed. This requires understanding current biodiversity patterns and threats, setting explicit conservation goals, and assessing the adequacy of already implemented conservation actions (Margules and Pressey 2000).

Within the large array of potential conservation tools, protected areas are the most effective and most critical instruments for biodiversity protection (Lovejoy 2006). The number of legally protected areas has increased substantially since the mid 20th century (Naughton-Treves et al. 2005; IUCN and UNEP 2012) and today they cover 13%, 7% and 1.4% of the entire land surface area, coastal waters and oceans, respectively (UNEP 2011). However, the development of reserve networks has in the past occurred in an *ad hoc* manner (Margules and Pressey 2000), with areas becoming protected due to their scenic or aesthetic values, or because they bear little economical importance to the human society (Pressey et al. 1993; Mendel and Kirkpatrick 2002). This approach has resulted in majority of the protected areas to be located in remote, unproductive and often biologically poor sites, leaving a substantial proportion of the global pool of species, communities and ecosystems unprotected (Brooks et al. 2004; Rodrigues et al. 2004). As a response the field of systematic conservation planning has rapidly generated sophisticated spatial prioritization methodologies which aim at cost-effectively increasing the representativeness of current reserve networks (e.g. Possingham et al. 2000; Moilanen et al. 2005) and to enhance long-term persistence of biodiversity in protected areas (Cabeza and Moilanen 2001; Noss et al. 2002).

To date, the field of systematic conservation planning has focused on threats such as fragmentation and loss of natural habitats, overexploitation (especially overfishing) and spread of invasive alien species. Assuming that species distribution patterns are static, these threats are often addressed by spatially prioritizing conservation actions across multiple optional locations. Climate change poses an entirely new challenge to conservation planning by forcing species to shift their distributions while protected areas remain geographically fixed (Millennium Ecosystem Assessment 2005; Lovejoy 2006; Pressey et al. 2007). For this reason together with their increasing isolation in a matrix of highly modified landscapes, protected areas of the present-day will not be enough to accommodate and buffer climate-induced changes in biota (Pressey et al. 2007; Heller and Zavaleta 2009). Hence, in addition to directly threatening the existence of numerous species, climate change can potentially foil past conservation achievements as already protected species are forced to move out from protected areas (Araújo et al. 2004). Changes of species composition in protected areas are already being observed (e.g. Kharouba and Kerr 2010), and forecasts for the near future predict major changes to take place during the 21st century (Burns et al. 2003; Thuiller et al. 2006; Hole et al. 2009; Araújo et al. 2011).

1.3. PREDICTIVE SPECIES DISTRIBUTION MODELLING

Understanding conservation needs in a changing world requires information about potential future impacts. Predictive spatial modelling provides a useful tool to estimate how species distribution patterns might behave under climate change. The large array of various modelling techniques can be roughly categorized into two groups: i) *mechanistic models* and ii) *niche models* which are also called *correlative models* (Morin and Lechowicz 2008). Mechanistic models are more complex, simulating detailed interactions between species and its biotic and abiotic surroundings under changing conditions [e.g. dynamic global vegetation models (Sitch et al. 2003; Prentice et al. 2007), gap models (Bugmann 2001) and PHENOFIT (Chuine and Beaubien 2001)]. These models allow sophisticated analyses

on how species' population size, dynamics and distribution react to climate change. Mechanistic models are, however, very data demanding, requiring detailed prior information about various ecological and physiological features of the species in question. As such information is rarely available the usage of mechanistic models in the climate change context has thus far been restricted to only a handful of species (Jeltsch et al. 2008).

The so-called niche models, also known as habitat suitability models or bioclimatic envelope models (BEMs), are a less data demanding option. These are statistical models that construct a correlative relationship between the known distribution of species and prevailing climatic conditions (Morin and Lechowicz 2008) [e.g. generalized linear models (GLM), generalized additive models (GAM), artificial neural networks (ANN) and classification tree analysis (CTA)]. The statistical correlation is then combined with information from future climate projections to analyse how species' climatic envelope moves across space through time. These models generally ignore several important biological factors such as species' dispersal capability, evolutionary processes, and species interactions (Thuiller et al. 2008) although recently steps have been taken to address these aspects (e.g. Araújo and Luoto 2007; Anderson et al. 2009; Morin and Thuiller 2009; Huntley et al. 2010). Due to their considerably lower information requirements niche models can be applied for a substantial number of species, allowing analyses about the expected climate change impacts on biodiversity patterns on large-scales and across multiple taxa (e.g.Berry et al. 2002; Thomas et al. 2004; Thuiller et al. 2005). In some studies they have been proven to be as powerful as mechanistic models (Morin and Thuiller 2009; Kearney et al. 2010). Furthermore, because of their broad applicability, conservation studies using niche models have thus far been most successful in communicating the potential dangers of climate change beyond the academic realm (IPCC 2007a; Araújo 2009). All modelling results presented in the following chapters have been obtained using niche models.

1.4. UNCERTAINTIES AND CHALLENGES

A major challenge in conservation planning under climate change is that it is hampered by uncertainty about future processes and our ability to correctly anticipate them. Predicting future actions of human society, which in turn largely dictate the development of GHG emissions, is obviously not a trivial task. To date scientists have been compelled to rely on a group of alternative but equally likely future scenarios (such as SRES scenarios, see Box 1), that explore potential development pathways covering a wide range of demographic, economic and technological drivers and result in multiple options for the future development of GHG emissions (IPCC 2000; Nakicenovic and Swart 2000; Arnell et al. 2004). Also, although the geo-physical processes that affect climate are already fairly well understood, there remain gaps in the knowledge of certain key drivers such as carbon cycle and cloud feedbacks, oceanic carbon uptake and behaviour of large ice sheet masses in Greenland and the Antarctic (IPCC 2007b). Therefore predicted changes in climate, especially beyond year 2050, are inherently coupled with uncertainty and depend strongly on the selection of emission scenario and climate model used to produce them.

When forecasting species distribution shifts, further uncertainties arise from the sensitivity of model results to the selection of niche modelling technique (Buisson et al. 2010). Although niche models are all based on the same principle, they differ in their technical details such as algorithms and parameterizations (Thuiller et al. 2004). Different niche model techniques have been shown to produce considerably different modelling results (Thuiller 2004; Diniz-Filho et al. 2009) where the variation stems mostly from their i) different usage of species presence-absence data (Elith et al. 2006), and ii) the various assumptions made by each algorithm when extrapolating environmental variables beyond the range of the data used to define the species-climate relationship (Pearson et al. 2006). Each of these models has its strengths and weaknesses but thus far none of the existing techniques have been shown to be superior when predicting future changes (Araújo et al. 2005b). In order to reduce the uncertainty stemming from selecting the 'correct' model, researchers now advocate the use of several modelling techniques to explore the resulting variation and to combine information across models with appropriate consensus methods (Araújo and New 2007). This framework of *ensemble forecasting* has gained attention in scientific literature as there are indications that it can produce more accurate predictions (Araújo et al. 2005a), but also because finding consensus results across multiple modelling techniques give better confidence about the robustness and usability of the forecasts. Nevertheless, ensemble forecasting addresses only uncertainties that arise from inter-model variation, and therefore provides no solution to the

uncertainties arising from data quality, details of statistical functions or the fundamental ecological assumptions behind the niche models. These aspects are discussed in more detail in Section 3.2.

With all these uncertainties, it is understandably difficult to conduct proactive conservation planning that accounts for climate change impacts. More importantly, it is difficult to convince decision-makers about the robustness of these planning results and the necessity to implement them. The uncertainty of climate change can significantly hinder the willingness of decision-makers to practice proactive conservation, especially when it comes with the trade-off of allocating scarce resources away from conservation actions that could successfully and with higher certainty protect biodiversity against present-day threats. The field of conservation planning is thus faced with a dilemma: Climate change is arguably a major threat to biodiversity and taking no action can lead to catastrophic outcomes. But investing in uncertain conservation actions to mitigate climate change impacts comes with a high risk of making wrong decisions, and thus wasting precious conservation resources. This thesis aims to assist in tackling this dilemma.

2. AIMS OF THE THESIS

The main aim of this thesis is to enhance our capability to protect biodiversity efficiently under changing climatic conditions. Increasing calls from scientists have demanded a rapid inclusion of climate change considerations to systematic conservation planning, underlining the need to shift from reactive conservation actions to a more proactive working realm. Several methodologies to predict and mitigate future impacts of climate change have been developed, however conservation actions utilizing these methodologies are still lacking. Major challenges for implementation relate to uncertainty about i) how climate change will develop in the future, and ii) whether we are able to anticipate its impacts on biodiversity accurately enough to allow proactive, yet effective conservation actions.

In this thesis I investigate the uncertainties in observing and predicting climate change driven impacts, and the risks and possibilities of conducting conservation planning under inherently uncertain future conditions. Ultimately, the work presented in this thesis addresses the following questions:

1. How do the different sources of uncertainty affect our understanding about climate change impacts and abilities to mitigate those impacts?
2. Are niche based models useful in predicting climate change impacts on biodiversity and its conservation?
3. Should we and could we do proactive conservation planning that accounts for near future climate change?

In the following thesis summary, I will also present some complementary results of the work which are not included in any of the chapters.

3. RESULTS AND DISCUSSION

3.1 MEASURING ONGOING CHANGES

One of the most commonly reported biological responses to recent climate change are distribution shifts of species (Parmesan and Yohe 2003; Walther et al. 2005; Parmesan 2006). Shifts can take place either along a latitudinal gradient, where ranges show poleward movements (Fig. 1), or along an elevation gradient, where ranges shift upwards to higher altitudes. Comparisons of present and historical distribution patterns as well as on-going monitoring schemes reveal that species are on the move: globally, it has been estimated that species from various taxa have shifted their ranges, on average, 16.6 km/decade polewards and 11.1 m/decade upwards in elevation since mid 20th century (Chen et al. 2011). Although the majority of studied species have shifted their ranges to a direction that is concordant with climate warming (Thomas 2010), there is substantial variation in the observed changes that include also contractions towards the equator and shifts to lower altitudes (Hill et al. 2002; Parmesan and Yohe 2003; Arribas et al. 2012). Overall the variation in observed patterns has been larger between species than between higher taxa (Chen et al. 2011), supporting previous conclusions that species tend to react individualistically to the changing climatic conditions (Huntley 1991; Williams et al. 2001). Notwithstanding the large variation in species' responses, emerging patterns suggest that particularly habitat generalists with good dispersal abilities have rapidly shifted their distributions together with changing climate patterns, whereas poor dispersers with specialized habitat requirements are more often lagging behind

or showing discordant responses (e.g. Warren et al. 2001; Julliard et al. 2004; Pöyry et al. 2009).

However, one should keep in mind that the data currently available for assessing species distribution changes are globally biased towards temperate and boreal regions (the so called *Wallacean shortfall*) and towards few well studied taxa (the so called *Linnean shortfall*) (Whittaker et al. 2005). Furthermore, it is challenging to reliably disentangle climate change driven distribution changes from other drivers such as habitat loss (e.g. Parmesan et al. 1999), natural variation (Robertson et al. 2010), or from observation biases (Tingley and Beissinger 2009). Thomas and Lennon (1999) introduced a method that statistically corrects observed range margin shifts with changes in distributions that could potentially be caused by other factors than climate (see **Chapter I**). As changes in species' range size automatically lead to changes in their range margins, the approach of Thomas & Lennon can be used to quantify whether species' ranges are shifting more than is expected based on changes in their range size. The Thomas & Lennon approach was originally designed to measure changes between consecutive atlases, which are considered the most powerful data to observe large-scale distribution shifts of species (Robertson et al. 2010, **Chapter I**). The method has been thereafter successfully used in several occasions to measure shifts in species' range margins (e.g. Hill et al. 2002; Brommer 2004; Gibbons et al. 2007; Pöyry et al. 2009; Zuckerberg et al. 2009).

The problem with the Thomas & Lennon (1999) approach is that it does not account for spatial and temporal changes in survey effort which can notably affect our understanding about the precise location of species' ranges. Knowledge about species distribution patterns is always distorted by observation errors (Shoo et al. 2006) which come mainly in two forms: *omission errors* and *commission errors*. Omission errors, which are more common, occur when species are falsely thought to be absent from a surveyed site, usually due to insufficient surveying of the site and/or elusive characteristics of the target species. Commission errors, on the other hand, occur when species are falsely thought to be present on a given site and are typically a result of misidentifications. In regrettably many past ecological surveys, including most of the existing atlas datasets, there have been no systematic recordings of survey effort (Tingley and Beissinger 2009; Robertson et al. 2010). Temporally varying survey effort in areas around species' ranges can therefore lead to false impressions of species expanding to new sites when in reality they were simply not detected during the first survey (Shoo et al. 2006; Robertson et al. 2010, see Box 2). As pointed out by a recent review by Tingley and Beissinger (2009), such potential errors in the studies focusing on species distribution changes are in most cases overlooked.

In **Chapter I** we re-investigated previously reported range margin shifts of breeding birds that have been produced using the Thomas & Lennon approach on atlas data from Great-Britain, Finland and New York State (Thomas and Lennon 1999; Brommer 2004; Zuckerberg et al. 2009). In this study, we found that if changes in survey effort are not explicitly accounted for, the observed range margin shifts can be in part a sampling artefact. Our results show that the Thomas & Lennon (1999) approach is not robust to spatiotemporally varying survey effort when changes in survey effort occur abruptly around species' range edges. The findings of **Chapter I** imply that the previously reported range margin shifts of breeding birds might be upward biased, particularly for Great Britain and Finland. The problem of uneven survey effort is also evident from the results of **Chapter II** where spatiotemporally varying survey effort between the Finnish bird atlases is likely to explain the relatively abrupt changes in range sizes of narrowly distributed species.

Uneven survey effort can significantly hinder our abilities to compare distribution patterns between consecutive points in time. This is particularly troublesome because not only does it obscure our understanding of species' responses to climate change (**Chapter I**), but it can also foil our attempts to validate the accuracy of models when comparing predictions to observed patterns (**Chapter II**). The findings of **Chapters I** and **II** highlight an urgent need to adapt more rigorous and systematic methods for measuring survey effort in ecological mappings. They also provide support for the emerging view that measurements of climate change driven distribution shifts should not be restricted to range edges (Shoo et al. 2006; Lenoir et al. 2008; Tingley and Beissinger 2009). For example, Shoo et al. (2006) argue that range centres might be more suitable study targets as they are less sensitive to both natural variation and changes in survey effort, and are more powerful in capturing smaller changes in comparison to range boundaries (see also Archaux 2004). It has been therefore suggested that monitoring occupancy changes across the whole distribution might prove to be a more informative approach when assessing species' responses to environmental changes (Lenoir et al. 2008; Tingley and Beissinger 2009).

Box 2. Survey effort and Finnish breeding bird atlases

Regional atlases are considered the most comprehensive sources of species occurrence data with standardized survey methodologies (**Chapter I**). Nevertheless, they are prone to observation errors as they usually cover large geographical areas (up to hundreds of thousands of square kilometres) and under limited resources are mostly collected by voluntary observers with varying skills and motivations (Robertson et al. 2010). As a result, survey effort among atlas cells varies both spatially and temporally. A further characteristic of atlas surveys is that data sampling is not randomized but tends to be opportunistic. That is, participants may be encouraged to reach certain objectives to achieve consistent and adequate effort (e.g. spending a minimum number of hours or detecting a pre-specified number of species).

The distributions of breeding birds have been mapped in Finland during three national surveys: 1974–79, 1986–89 and 2006–10. During the second atlas project (1986–89) surveyors were encouraged to put special effort to atlas cells that in the first atlas (1974–79) remained poorly studied (Väisänen *et al.* 1998). Consequently, the number of observations increased especially in northern and eastern Finland in the second atlas (Väisänen et al. 1998, Fig. 2a). The fact that survey effort has not been directly measured in the Finnish atlases is problematic, because the northern range limits of many southern species in Finland are located

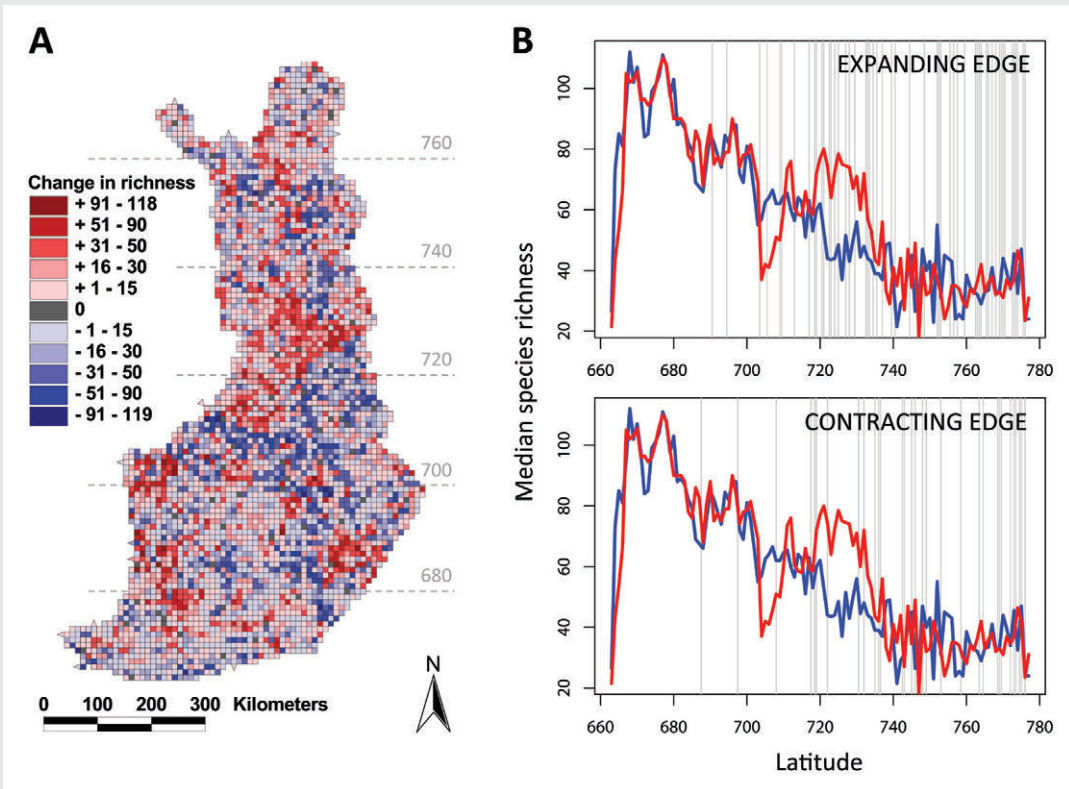

Figure 2 | Spatial and temporal changes in species richness between the first (1974–79) and second (1986–89) bird atlases in Finland. Panel **a.** shows whether the recorded species richness has been higher in the first atlas (blue colours) or in the second atlas (red colours). Dashed lines indicate latitudinal reference points, measured as 10 km from the equator. Panels in **b.** show median species richness in Finnish atlas cells across latitude. Blue line: first atlas, red line: second atlas. Grey vertical lines indicate the locations of northern boundaries of those southern species that have either moved northwards (expanding edge) or moved southwards (contracting edge). For species expanding northwards, latitude of the northern edge was calculated from the second atlas (i.e. from the latitudes where species had appeared to), and for contracting species from the first atlas (i.e. from those latitudes the species had disappeared from).

in the exact regions that were more poorly mapped in the first atlas than in the second. This is illustrated in Figure 2b, which shows that the median latitudinal species richness in Finnish atlas cells changed very unevenly between the first and second surveys with marked peaks in areas where survey effort was intensified (particularly latitudes of 7100-7400km north from the equator). For several of the southerly species, which Brommer (2004) reported to have shifted their ranges between first and second atlas, the 'new' northern margins coincided with these latitudes (Fig. 2b, upper panel). It is therefore reasonable to presume that the intensified surveys in these regions yielded in the detection of species that had not been observed in the areas before, creating a false impression of an expanding range. This view is further supported by the observation that almost no species seemed to contract their northern ranges from these regions (Fig. 2b, lower panel).

3.2. PREDICTIONS AND OBSERVATIONS – DO THE MODELS WORK?

Our ability to create a 'perfect' model for predicting species distribution shifts is hampered by several factors: Firstly, and surprisingly often, we do not have comprehensive information about species' current distributions (Whittaker et al. 2005). In many cases the biological data upon which models are built have poor sample size and are spatially and environmentally biased (Araújo and Guisan 2006). Secondly, niche models are based on an empirical relationship between the observed distribution of species and climatic variables, and often ignore non-climatic factors such as interspecific competition that also constrain current distributions. (Guisan and Zimmermann 2000; Pearson and Dawson 2003). Hence, niche models portray only an approximation of the species' climate envelope (for discussion about the niche concept in bioclimatic modelling see Araújo and Guisan 2006). Thirdly, despite the rapid development of modelling techniques, there is still a need to enhance our understanding about how to build and parameterize models to correctly reflect distribution patterns across multiple species (Elith et al. 2006; Liu et al. 2010). Finally, for the majority of biodiversity we do not know whether the current distribution patterns reflect a quasi-equilibrium state between species and climate, or if some species might still be in the process of responding to previous climatic changes such as the last glacial maximum (Svenning and Skov 2004). If species are not in equilibrium with their climate, models built upon current distribution patterns will not be able to describe the true species-climate relationship (Guisan and Thuiller 2005).

Even if we were able to construct a perfectly modelled species-climate relationship, there remain significant unknowns in predicting future distribution patterns. It is likely that climate change will create entirely novel climatic conditions, that is, new combinations of climatic characteristics which might change beyond currently known scale limits (Garcia et al. 2012). The ability of the models to extrapolate species' responses to these new conditions is not known (Araújo et al. 2005a; Elith and Leathwick 2009). A related and highly debated question is also whether the current link between species and climate will be maintained through time, or whether this relationship is likely to be dynamic and evolve under changing environmental conditions (Wiens and Graham 2005; Pearman et al. 2008b). One of the key assumptions behind predictive niche modelling is that species-climate relationships are static (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Pearman et al. 2008b) and by default they do not account for dynamics in the fundamental niche driven by, for example, evolutionary processes. Finally, we do not know how simple correlative models based on climatic variables are able to predict distribution shifts driven by additional factors, such as biotic interactions between species and species' dispersal events (Pearson and Dawson 2003). Particularly at local scales other drivers such as land use changes or interspecific competition might be more important determinants of species' occurrences (Davis et al. 1998; Lawton 2000).

Several of the points listed above have been extensively studied and methods to address these uncertainties are rapidly being developed (e.g. Hoffman and Kellermann 2007; Williams and Jackson 2007; Phillips et al. 2009). A critical question still remains about how to evaluate the successfulness of predictions when data from the future to validate model results do not exist (Araújo and Rahbek 2006). Studies have shown that good model performance when predicting present distributions does not guarantee good performance when using the same model to predict future distributions (Araújo et al. 2005a), and hence traditional model validation methods cannot be trusted. One option to validate model performance is *hindcasting* where species distributions are predicted back in time (Prentice et al. 1991; Martínez-Meyer

et al. 2004; Pearman et al. 2008b). In this approach models are calibrated using present-day information about species' occurrences and prevailing climatic conditions, and then tested by predicting historical distributions reconstructed from fossil records. Another option is to *substitute time with space*, i.e. calibrate models using species information from one region and then predict occurrence of the same species in another region (e.g. Beerling et al. 1995; Randin et al. 2006). Results from studies looking at the transferability of models through space (time-for-space substitution) or time (hindcasting) have been diverse. Exercises transferring niche models through space have shown large variation in predictive performance both between species (Pearman et al. 2008a) but also within the global range of singular species (Broennimann and Guisan 2008). Studies investigating transferability through time have provided more scope for optimism as in some cases niche models have successfully predicted historical distributions (e.g. Martínez-Meyer et al. 2004), supporting the idea that species-climate relationships are temporally robust (i.e. *niche conservatism*, Wiens and Graham 2005).

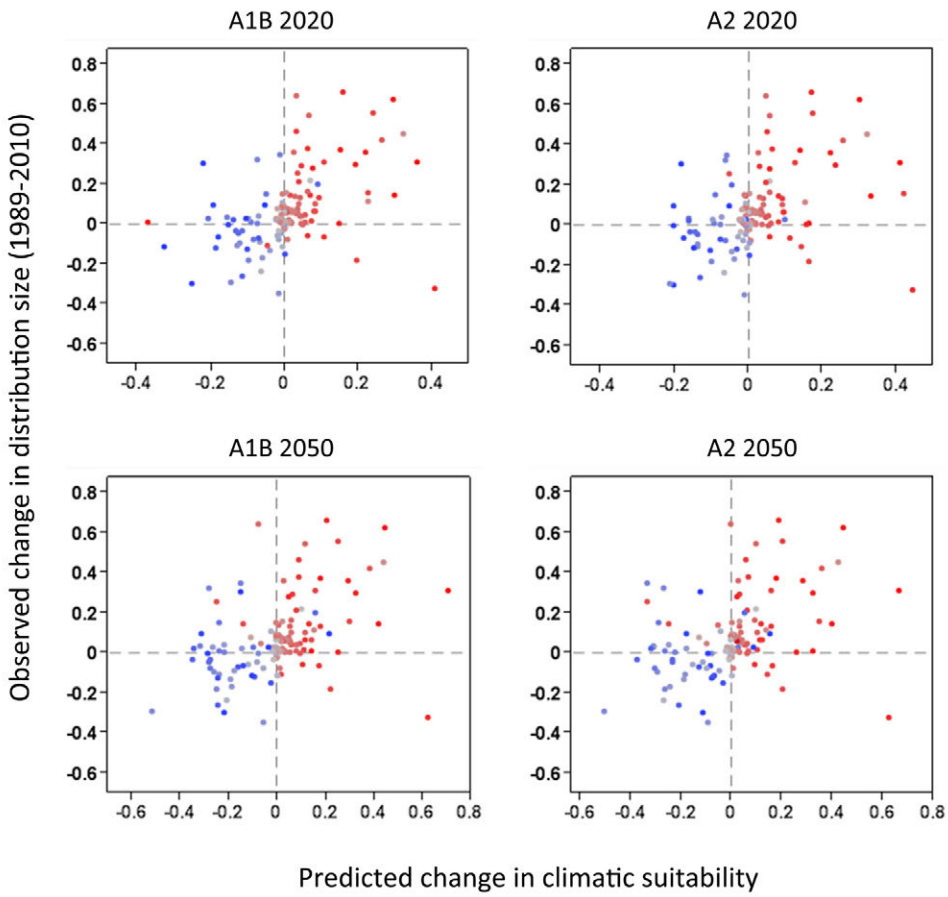

Figure 3 | Observed and predicted changes in the national distributions of Finnish breeding birds. Each point represents one species. The colour of data points corresponds to the latitude of the weighted centre of species distribution during the 1970s, showing the most southern species as red and the most northern species as blue. The Y-axis in the panels show the observed change is species' distribution size, measured as the $\log_{10}$-ratio of occupied atlas cells in the third (2006-10) atlas over the number of occupied atlas cells in the pooled first and second (1974-89) atlas. Hence, positive values indicate observed increases in distribution size whereas negative values indicate observed decreases. Similarly, the X-axis shows the predicted change in climatic suitability under two different climate scenarios (A1B and A2) and two time periods (1990-2020, and 1990-2050), measured as the $\log_{10}$-ratio of sum of probabilities (of occurrence) in each atlas cell in the future over the sum of probabilities in the present. For details see **Chapter II.**

Yet, others have reported larger variation in the predictive performance of the models (Randin et al. 2006; Pearman et al. 2008b), arguing that simple generalizations about the goodness of niche models under varying climatic conditions cannot be made.

A more optimal approach for model validation is to compare modelled results to the observed changes which have taken place during the time period of recent climatic warming, i.e. in the recent past (Araújo et al. 2005a). The obvious problem with this approach is that temporal data, covering important climatic changes as well as associated impacts on species are rarely available (Araújo et al. 2005b; Duncan et al. 2006, see also Warren et al. 2001, but note that here observations were not used for model validation). **Chapter II** presents a new comparison on how changes in the national distributions of Finnish breeding birds correlate with modelled predictions based on consensus forecasts across eight niche models (Fig. 3). Observed changes between 1989 and 2010 corresponded well to the modelled predictions done for a roughly similar time scale (1990–2020). In general, results from **Chapter II** showed strong evidence that i) large-scale distribution shifts of Finnish birds are already taking place, and ii) these shifts follow the modelled expectations. Additionally, the largest variation observed in the match between predicted and observed changes was related to the rarity or small distribution size of species (Fig. 2c in **Chapter II**). Note however that this mismatch is not necessarily driven by the poor performance of the models, but could also be explained by changes in survey effort between atlases, which can cause seemingly abrupt relative changes in the range size of narrowly distributed species (Robertson et al. 2010, see also section 3.1). Logically, the observed patterns followed predictions done for similar time period (1990–2020) better than predictions done further into the future (2012–2050), albeit it should be noted that the predicted changes under all scenarios and time scales significantly explained the observed changes (**Chapter II**). This implies that niche models can provide useful information about the future events for which no validation data exist.

Recently population trend data have also been used to evaluate the match between observed changes in abundance and predicted contractions and expansions in species distributions under climate change (Green et al. 2008; Gregory et al. 2009; **Chapters II** and **III**). As abundance is known to correlate with distribution size (e.g. Brown 1984; Gaston et al. 1997; **Chapter II**) population trends can reflect ongoing changes in species distributions, especially on the expanding and contracting range margins, when actual distribution data is not available. Moreover, population trend data provide an interesting additional information source to evaluate climate change impacts as monitoring schemes can be performed with higher temporal resolution (i.e. annual monitoring) in comparison to national or regional atlas mappings, which typically take years to finish and are replicated in decade long intervals. Trends can therefore provide early indication of species' responses to the changing climate. However, population trend data are also more sensitive to natural yearly variation in climatic conditions as well as to non-climatic drivers (Balmford et al. 2003; Loh et al. 2005), which should be kept in mind when interpreting observed changes in species abundances.

Gregory et al. (2009) have shown that at the European scale population trends of land birds have since the beginning of 1980s developed in correspondence with expected distribution changes under climate change by the end of 21st century. **Chapters II** and **III** show that population trends of common breeding birds correlate positively with future predictions also at the national scale. However this relationship is weaker than comparisons made with observed distribution changes (**Chapter II**), potentially reflecting the higher sensitivity of abundance data to non-climatic drivers. On the other hand, population trend data can reveal more subtle changes that are not necessarily captured by distribution data. For example, in **Chapter II** comparison between predictions and population trends showed that particularly the population sizes of long-distance migrants have decreased more than what could be expected based on the models. Also Gregory et al. (2009) report significant co-variation of predicted future changes and migratory behaviour but do not specify its nature. The findings of **Chapter II** are in line with several recent studies that report decreasing population trends among migratory birds (Sanderson et al. 2006; Brommer 2008; Gregory et al. 2009). It is therefore becoming increasingly clear that evaluation of climate change impacts on migratory species should not be restricted to national ranges alone, but that they need to span across the entire migratory route.

When validating future predictions, an interesting aspect is not only the degree of congruence between predicted and observed changes, but also

the temporal dimension of the agreement. In their study with European land birds, Gregory et al. (2009) showed that the degree to which population trends corresponded to future predictions changed through time. Interestingly, they found that species' population trends began to evolve in parallel with predicted changes only after the mid-1980s, which corresponds to the starting point of increasing average temperatures in Europe (Gregory et al. 2009). In **Chapter II** we found patterns that support the results of Gregory et al. (2009) as modelled predictions showed no match with observed distribution patterns that took place between 1970s and 1980s, but correctly predicted changes only after 1980s (Fig. 2 in **Chapter II**). However, due to spatiotemporally varying survey effort between the Finnish atlases (see Section 3.1. and **Chapters I** and **II**), these findings must be interpreted with caution.

An interesting detail that emerged from the Finnish breeding bird studies is that observed changes from the past few decades seemed to be more accurately following predictions done with A1 climate scenarios. In **Chapter III**, population trends showed strongest correlation with predictions done under scenario A1FI. Similarly, in **Chapter II** both population trends and the observed changes in species distributions matched better with predictions done under A1B rather than scenario A2. Note that although A2 scenario is expected to lead to a larger change in climate by the end of 21st century, until the year 2050 greenhouse gas (GHG) emissions are predicted to be higher in A1B (Nakicenovic and Swart 2000). These results therefore suggest that species are responding to changes in climatic conditions which follow the most extreme predictions done by IPCC, although it should be noted that differences between A1 and A2 scenarios were not considerably large (**Chapters II** and **III**). Nevertheless, the results correspond to the recent finding that since the year 2000 global GHG emissions have followed the most carbon intensive SRES scenario A1FI (Le Quéré et al. 2009). These findings are alarming as they imply that we are heading towards the most drastic changes in the global climate system.

3.3. ROBUST SPATIAL CONSERVATION PRIORITIZATION IN A CHANGING WORLD

3.3.1 Should we account for climate change?

The central challenge in today's systematic conservation planning is to understand how areas should be prioritized for protection as species are shifting their distributions, while keeping in mind that the existing global reserve network provides a biased sample of both biodiversity (Rodrigues et al. 2004; **Chapter III**) and environmental conditions (Scott et al. 2001; Mendel and Kirkpatrick 2002). The high uncertainties related to future climate change and its ecological consequences have created a debate about whether and how modelling results should be used in spatial conservation prioritization (e.g. Hulme 2005; Hannah et al. 2007). Some have argued that due to the tremendous uncertainty in predicting the future, scarce conservation resources should instead be used to protect large areas that are presently known to be of high quality, environmentally heterogeneous and which mitigate other threats posed by human actions (Hulme 2005; Pyke and Fischer 2005; Hodgson et al. 2009). But would these areas be enough to safeguard species under changing climate (Box 3)?

Empirical data to validate different conservation strategies do not yet exist, but models can provide some valuable insights about what might happen if future dynamics were entirely ignored. For example, Pyke et al. (2005) found that although the existing reserve network of Cape Floristic Region in South-Africa currently captures a fairly balanced representation of different climatic conditions, the network is unable to sustain its level of climatic heterogeneity by 2050 under climate change. Indeed, several studies predict that existing reserve networks will face large turnovers in their species compositions (Dockerty et al. 2003; Thuiller et al. 2006; Hole et al. 2009). Could this be due to the fact that such networks have not been selected in the most optimal way? Araújo et al. (2004) found that even if the current protected land areas were optimally re-distributed using present knowledge about biodiversity patterns and modern conservation prioritization methodologies, the resulting reserve network would not be able to buffer climate change impacts. Using European plant species as an example, they showed that artificial reserve networks created with six modern site selection methods would lose 6-11% of the species they were designed to protect by the year 2050. This despite the fact that expected impacts of climate change on European plants were predicted to be fairly modest, as 93% of the studied 1,200 species would have overlapping present and future distribution, and only 5% would lose their entire climatically suitable space. Interestingly,

these networks failed to retain species under changing conditions even when the methods were set to prioritize present habitat quality or resulting protected area size (Araújo et al. 2004).

In the real world reserve networks cannot be optimally selected from the beginning, but any reserve selection procedure must rely on the expansion of already existing protected area networks. Normally, in order to allocate scarce resources efficiently, the first step would be to use tools to identify which features (i.e. which habitat types, species or environmental features) are still unrepresented or under-represented in existing protected areas and consequently in need for further protection (Margules and Pressey 2000). However, in a highly dynamic world with changing biodiversity patterns our understanding on what is already protected and what is in need of further protection will quickly become distorted. In **Chapter III**, using the Finnish protected areas and breeding birds as a case study, we explored how tools for identifying conservation priorities would perform when near future dynamics are ignored.

The results from this study show that if only static information about species' current distributions is considered, conservation recommendations resulting from these conventional analyses might not correctly reflect the actual conservation needs of the species. In **Chapter III** we found that when information about ongoing and future dynamics was ignored, the analysis flagged several southerly species and habitats as under-represented in Finnish protected areas, thus identifying them as next conservation priorities. However, additional information about population trends revealed that many of these species were actually expanding in terms of population size. At the same time majority of the northerly species were declining despite having the largest coverage in protected areas and being identified as well protected. Furthermore, population dynamics correlated with modelled future changes in species' climatic suitability, implying that Finnish breeding birds were already responding to the changing climate. According to modelled impacts of climate change by 2050, several of the northerly species are expected to contract and potentially disappear from Finland. Similarly, many southern species are expected to expand their ranges to northern parts of the country where their conservation status is likely to be positively developed due to the large protected areas in this region.

The results of **Chapter III** raise two important points. First, our findings with Finnish breeding birds repeat the alarming message reported in previous studies that current protected areas, regardless of their size and aggregation, are unable to buffer pressures caused by large-scale environmental changes (Dockerty et al. 2003; Hannah et al. 2007). Second, the very tools designed to guide us how to efficiently and effectively protect biodiversity can be misleading when ongoing and near future dynamics are not accounted for. In order to understand the coming changes caused by warming climate, and how to best mitigate impacts of climate change on biodiversity, conservation planners and managers would benefit substantially from the information provided by ongoing monitoring programs (such as population surveys) and modelling future distribution shifts. Furthermore, the case of Finnish breeding birds questions the rationale of spatial conservation prioritization based on information from the present-day only (Box 3). For example, if the Finnish reserve network was to be complemented with additional protected areas, what should be the criteria for selecting these new sites for protection?

Most importantly, it has been shown that ignoring climate change impacts will eventually lead to more costly and less effective conservation outcomes. Hannah et al. (2007) conducted a conservation planning study across multiple taxa and in three different regions where they identified complementary sites to existing reserve networks in order to achieve a full representation of each regions' species pool. In the course of the study they compared the costs of two optional conservation strategies, where future impacts of climate change were either i) immediately anticipated and integrated to protected area selection together with species' current distributions (one step action), or ii) initially ignored and accounted for only after species' current distributions were efficiently protected (two-step action). Their results show that sequential two-step conservation strategy required 1.2 - 1.7 times more land area to meet the conservation targets than if site selection was based on both present and future distributions from the beginning (Hannah et al. 2007), strongly advocating a paradigm shift to more proactive conservation planning. Accumulating evidence shows that, despite their uncertainties, the modelled predictions are in congruence with species' responses to climate change (Araújo et al. 2005b; Green et al. 2008; Gregory et al. 2009; **Chapters II** and **III**) and they can be highly informative in conservation planning when correctly used.

Box 3. Do your best today and hope that it works out?

As modelling future impacts is inherently an uncertain process, some researchers have suggested that one strategy could be to protect sites that are of high quality now, as it is likely that they will remain biologically good also in the future even if the species pool of the site might experience changes (e.g. Hodgson et al. 2009). I tested this hypothesis using Finnish breeding birds as an example and identified the top 10% conservation priorities for Finland according to species' current distribution patterns, weighting all species equally and excluding species of agricultural and built-up habitats (n=38, see **Chapter III** for details about the distribution data used). The prioritization was done with conservation software Zonation v. 2.0 (Moilanen et al. 2005; Moilanen and Kujala 2008) which produces a hierarchal ranking of landscapes balancing the outcome across multiple species (see **Chapter IV**). The areas of highest priority across species can then be identified simply by taking any given amount of area with highest priority ranks. I evaluated how well sites included within the best 10%, an area roughly equal to current Finnish reserve network, would retain species distributions by 2050 under climate change, following the climate scenario A1FI and assuming that species will occupy their entire climatically suitable space in the future (see **Chapter III** for details about the modelled distribution data used).

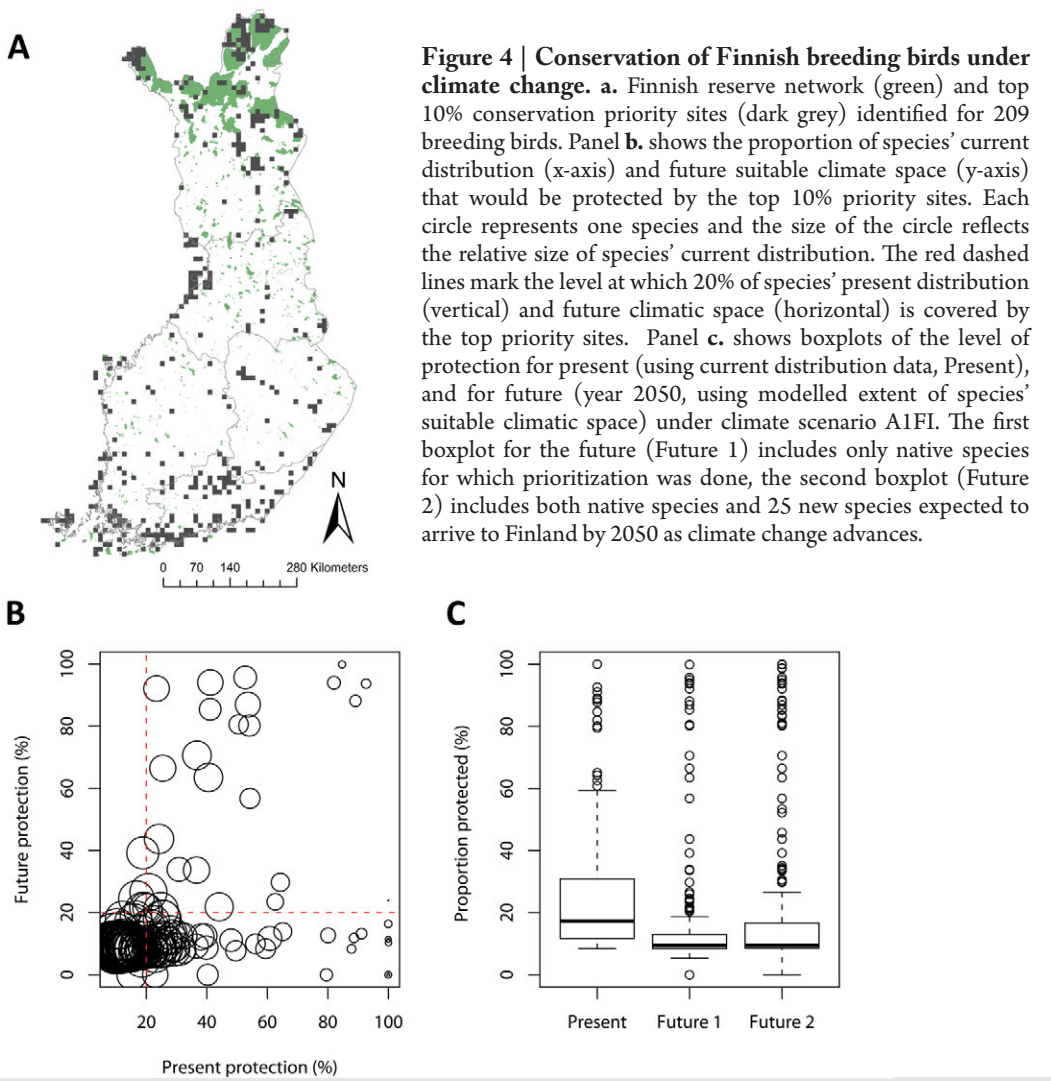

Figure 4 | Conservation of Finnish breeding birds under climate change. a. Finnish reserve network (green) and top 10% conservation priority sites (dark grey) identified for 209 breeding birds. Panel **b.** shows the proportion of species' current distribution (x-axis) and future suitable climate space (y-axis) that would be protected by the top 10% priority sites. Each circle represents one species and the size of the circle reflects the relative size of species' current distribution. The red dashed lines mark the level at which 20% of species' present distribution (vertical) and future climatic space (horizontal) is covered by the top priority sites. Panel **c.** shows boxplots of the level of protection for present (using current distribution data, Present), and for future (year 2050, using modelled extent of species' suitable climatic space) under climate scenario A1FI. The first boxplot for the future (Future 1) includes only native species for which prioritization was done, the second boxplot (Future 2) includes both native species and 25 new species expected to arrive to Finland by 2050 as climate change advances.

The top 10% priority sites identified by Zonation across 209 breeding birds were more evenly distributed across Finland in comparison to existing protected areas (Figure 4a). These sites represented all species included in the analysis, and effectively covered on average 32% (median 18%) of species' known distributions (Figure 4c). As species ranges would eventually shift due to climate change, their protection would undergo notable changes. Simple metrics from the analysis show that a large number of species for which the priority sites based on present distributions achieved high coverage, had less than 20% of their distributions protected by 2050 (Figure 4b). Similarly, for several species the level of coverage increased. Species with small or medium current range sizes were most affected by the expected range shifts, whereas for widely distributed species there were only marginal changes in the level of protection. The latter result is logical, as the most common species that currently occupy nearly the entire Finland will in most of the cases continue to do so in 2050.

However, if the priority sites identified in this analysis were to be protected, eight species would lose their entire protection by the year 2050, including Finnish red listed gyrfalcon (*Falco rusticolus*, EN), peregrine (*Falco peregrinus*, VU), purple sandpiper (*Calidris maritima*, VU), yellow wagtail (*Motacilla flava*, VU), barred warbler (*Sylvia nisoria*, EN) and guillemot (*Uria aalge*, EN). Furthermore, looking across the species pool, there is a net loss in the proportion of species distributions covered by the top priority sites within the study period (Figure 4c). This net loss remains even if one accounts for the possible new species (n=25) that could arrive to Finland due to climate change and would potentially occupy some of the southern priority sites.

As the modelled future conditions do not portray actual distributions of species, but their climatically suitable space, the results of this simplified exercise should be interpreted with caution. As such, the present and future levels of protection are not entirely comparable and the detailed figures should not be taken as the only view on how the future of Finnish bird conservation will develop. Nevertheless, the qualitative results do not support the arguments that simply protecting good present sites would safeguard species' future distributions. On the contrary, the results of this analysis provide support to the views that future impacts should be explicitly accounted for in spatial conservation prioritization (Araújo et al. 2004; Hannah et al. 2007; **Chapters II**, **III** and **IV**).

3.3.2. Could we account for climate change?

Robust conservation prioritization under climate change should ideally result in a set of protected areas which guarantee the persistence of species in the long term. In order to achieve this we would need to identify areas that are important for species' current and future distributions (i.e. of high quality), and that most effectively assist species to disperse from their current locations to areas that will be suitable in the future (i.e. good connectivity or aggregation of the reserve network). Furthermore, the quantity and sizes of protected areas should be large enough to allow long term persistence of multiple species under varying natural population dynamics and stochastic events. An important aspect is also where within species' present distributions conservation actions should be targeted: to leading range edges, where species are most likely to disperse to new sites (Parmesan 2006), or to distribution cores, where species have their highest abundance (i.e. higher likelihood to persist) and larger genetic variation to enhance adaptation (Willis and Birks 2006; Heller and Zavaleta 2009)?

Niche models can be used to address the question of species' future distributions (see section 3.2, **Chapters II**, **III** and **IV**), but they offer little help regarding aspects of dispersal or population dynamics. The majority of studies predicting species' future distribution shifts have utilized fairly simple dispersal frameworks, assuming either no-dispersal or full-dispersal scenarios (e.g. Araújo et al. 2004; Thomas et al. 2004; Thuiller et al. 2005). In the former case, the species is assumed to occupy only those areas that are modelled to remain climatically suitable throughout the time period in question. Similarly, in the latter scenario all areas with suitable climate in the future are assumed to become occupied by the species. The approach is understandably not very realistic, but without reliable information about dispersal capabilities of several hundreds of species this simplified approach can give useful insights by setting upper and lower limits across all potential dispersal options.

A more sophisticated approach was introduced by Williams et al. (2005) that used sequential predicting of species distribution shifts to identify dispersal

corridors under climate change for *Proteaceae* plant species in South-Africa. In this exercise species were first grouped to two dispersal distance classes depending on whether they were known to be wind dispersive (400m/year) or vector dispersive (i.e. dispersed by ants or rodents, c.a. 130m/year). Then, for each species the location of suitable climatic space was modelled in 10 year intervals and potential dispersal routes between consecutive time slices were identified according to species' biological dispersal capabilities. Finally, suitable climate corridors were selected by optimizing dispersal routes across all species to minimize the area required for protection, but in such a manner that each species would retain at least 100 km2 of their ranges during each time step. This approach is biologically more meaningful than mere comparison of dispersal extremes, and introduces significant amount of precision to the results. However, high level of precision comes with the cost of high uncertainty due to several underlying assumptions, such as whether the magnitude and pace of climate change follows the predictions and whether species' dispersal capabilities are correctly estimated. Evidence from real-life experiments show that there is also considerable uncertainty about how successfully species' movements are in the end facilitated by corridor type structures in the landscape (Halpin 1997; Ovaskainen et al. 2008). Furthermore, species cannot persist in corridors which are usually narrow stretches connecting habitat patches of species' actual occupancy. Network of corridors for multiple species can also require acquisition of substantial land stretches. This can easily divert scarce conservation resources away from protecting the core habitats of species from which their persistence is dependent on.

Another option to facilitate species' dispersal under climate change is to increase the general aggregation of reserve networks by selecting additional protected areas in a manner that increases connectivity. In highly connected landscapes species are known to have the highest actual and effective (genetic) population sizes, are least likely to become extinct, and also have the greatest likelihood of colonizing fresh habitat that is created either naturally or by human intervention (e.g. by restoration) (Debinski and Holt 2000; Hanski and Ovaskainen 2000). A metapopulation-type connectivity measure (Hanski 1998; Moilanen and Nieminen 2002) provides a fruitful basis for this approach as it efficiently combines information of both distance between suitable areas and their respective quality. Furthermore, the measure is scaled to match species-specific dispersal capability to guarantee its biological meaningfulness (Hanski 1998). Instead of explicit paths or corridors this approach can be used to identify high quality areas from species' present distributions that are within species-specific dispersal distance from high quality areas of species' future distributions (Rayfield et al. 2009; Carroll et al. 2010; **Chapter IV**). Implementation of such connectivity measures to conservation prioritization software such as Zonation (Moilanen et al. 2005; Moilanen and Kujala 2008) allows efficient prioritization of sites across multiple species and large geographical scales. We illustrate the usage of this approach in **Chapter IV**, where we identify priority conservation sites for European amphibians and reptiles under climate change. In this chapter the metapopulation-type connectivity was used to identify i) sites within species' current distribution which are well connected to high quality future sites and are expected to act as sources for the forthcoming distribution shift, and ii) sites within species' future distributions that are well connected to high quality present sites and can act as stepping stones facilitating species' dispersal to future core areas. Areas were then prioritized based on their conservation value as present core, source, stepping stone or future core across 106 herptile species, balancing the solution between distribution edges and cores (**Chapter IV**, Fig. 5).

However, like the approach introduced by Williams et al. (2005), also the metapopulation-type connectivity approach suffers from uncertainties in the development of future climate change as well as species' capability to disperse to new areas. **Chapter IV** introduces a framework where in addition to species distribution shifts and connectivity needs the conservation prioritization accounts for i) alternative climate change scenarios and their impacts, ii) uncertainty in the modelling of species distributions under present and future conditions, and iii) different levels of confidence about present and future. In this framework robustness of niche model predictions was increased by taking an ensemble mean across four different modelling techniques and prioritizing sites with high agreement between the models. Sites that are simultaneously of high quality and high certainty (i.e. high agreement between models) were then used to prioritize areas that are important as present cores, sources, stepping stones or future cores across all species. Conservation prioritization simultaneously for all possible future climates is not necessarily a sensible strategy, as the climatic conditions in each scenario become increasingly spatially dissimilar with time (Box 1). Hence, optimizing a solution to cover all possible futures

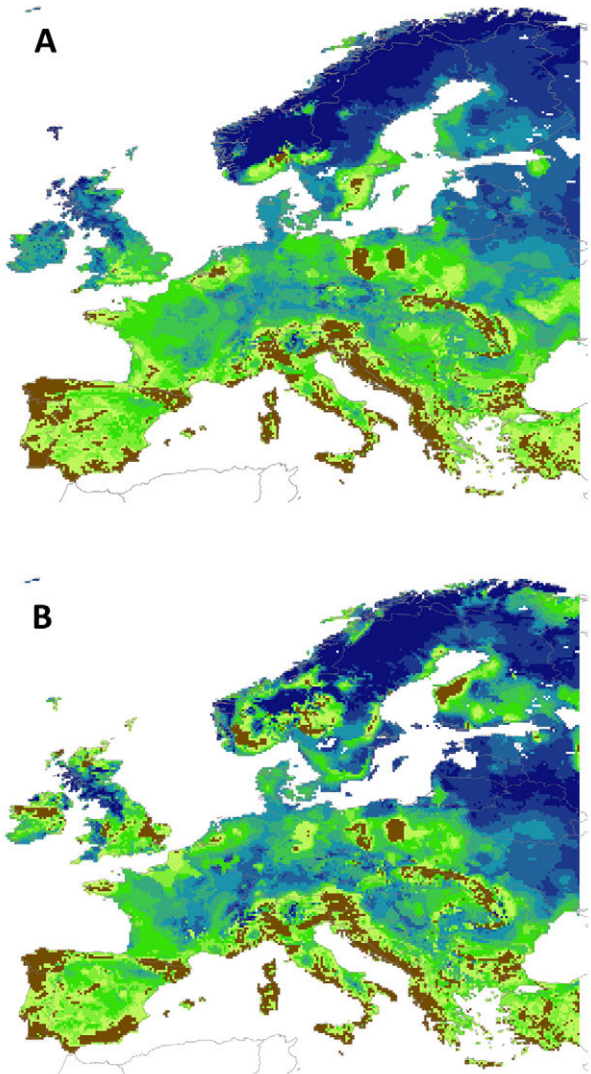

Figure 5 | Spatial prioritization for European amphibians and reptiles under climate change scenario A1FI. Prioritization was made across multiple species by accounting simultaneously for species' i) present cores, ii) future cores, iii) connectivity from present to future, and iv) connectivity from future to present. Colours from blue to light green show increasing priority across all species, brown areas indicate the best 10% of entire landscape. Panels show prioritization results when future distributions have been modelled for **a.** 2050 and **b.** 2080. See text and **Chapter IV** for details.

would be very inefficient as eventually only one of the scenarios will become reality and resources used to cover other scenarios are lost. For this reason, we conducted the prioritization separately for each SRES scenario and compared their overlap. Importantly, we also performed a cross-evaluation of potential risks and opportunities, which follow in a case when prioritization of areas is done with a 'wrong' scenario.

Conservation exercises that account for climate change impacts frequently neglect the point that knowledge about the past and present is much more certain and accurate than knowledge about the future (e.g. Hannah et al. 2007; Carroll et al. 2010; Carvalho et al. 2011). In **Chapter IV** we explored this aspect by constructing trade-off curves to show how much additional gain in future protection can be achieved when increasing weights are assigned to future distributions in the prioritization process. As increasing weight to the future can cause losses in the protection of species' present distributions, these trade-off curves can efficiently and transparently guide decision-makers to define a suitable level of loss that can be tolerated in order to enhance species' future protection. Results from **Chapter IV** thus show how robust prioritization can simultaneously be made for both present and future

by accounting for several uncertainties and without trading off too much from the conservation of species' present distributions. Note that in **Chapter IV** we did not explore the sensitivity of the results to different dispersal capabilities of species, but instead used a single measure across the species pool. The framework does allow species-specific dispersal values to be implemented if such detailed information is available. However, it has been suggested that uncertainties related to correctly estimating species' dispersal abilities may be far smaller than uncertainties arising from different reserve selection methods (Araújo et al. 2004).

3.4. WHERE ARE THE TRUE UNCERTAINTIES?

The studies presented in this thesis address various aspects of uncertainty, such as measurement errors in data (**Chapters I** and **II**), uncertainty about model performance and methodologies (**Chapters I, II, III** and **IV**) and gaps in our knowledge about future events (**Chapter IV**). But within the framework of conducting efficient and successful conservation under climate change the question of uncertainty is not restricted to the mere technical aspect of how to reliably predict and anticipate future changes. Further uncertainties arise when conservation methods and recommendations are put into practice.

Although several approaches to anticipate and plan for conservation impacts of climate change have been proposed (Heller and Zavaleta 2009), conservation actions utilizing these approaches and methods are to date non-existent. This can be partly explained by the novelty of the field, but it should be acknowledged that a similar phenomenon has become to dominate the entire domain of conservation biology (Prendergast et al. 1999; Knight et al. 2008). Knight et al. (2008) describe this problem as the *research–implementation gap*, also more generally known as the *knowing–doing gap* (Pfeffer and Sutton 1999), reflecting the significant division between conservation researchers and managers (Prendergast et al. 1999) and the fact that many of the techniques proposed by academia have not been tested nor proven by implementation (Knight et al. 2008).

Causes of the research–implementation gap arise from several sources. Pendergast et al. (1999) argued that the main reason for the lack of adapting sophisticated conservation tools is the poor level of communication: many conservation practitioners are simply not aware of the tools or their effectiveness (Pullin et al. 2004). Similarly, researchers are not aware of which real-life conservation questions they should most critically address, and many times the outputs of conservation science do not match the needs of conservation practitioners (Knight et al. 2006). Indeed, most of the scientific peer-reviewed publications do not report (Maddock and Benn 2000) or even discuss (Knight et al. 2008; Heller and Zavaleta 2009) implementation of the methods they present. Several studies have stated that the research-implementation gap is partially maintained by institutional structures of academia, where career developments of scientists hinge upon publishing articles in high-impact journals that eschew implementation (Campbell 2005).

Many others point out that the successfulness of any conservation method to be implemented depends on a much wider array of factors than a mere gap between conservation researchers and practitioners. It has been widely argued that one of the key reasons why several science-based methods and recommendations remain ignored is because they lack socio-political context, rendering them socially and politically naïve and exposing them to backlashes (Ludwig et al. 2001; Brechin et al. 2002; Ostrom 2007; Polasky 2008; **Chapter V**). Some go even as far as to say that academia has simply failed to convince the society why biodiversity should be protected in the first place (Watson 2005). There is a growing acceptance that environmental problems cannot be solved with natural sciences only, but efficient conservation actions require simultaneous understanding of human behaviour, culture, social structures and governance (Rittel and Webber 1973; Walters and Maguire 1996; Ludwig et al. 2001; Cowie and Borrett 2005; Curtis et al. 2005; Pahl-Wostl 2005). Just like there are uncertainties associated with climate change and its ecological consequences, there are severe uncertainties that affect policies and decision making in the management of global biodiversity conservation (Nakicenovic and Swart 2000; Ludwig et al. 2001; Van Der Sluijs et al. 2005; Ascough II et al. 2008). All these different aspects affect how we as a society decide that actions are needed, and implement policies that lead to successful conservation outcomes.

Understanding and reducing uncertainty has been one of the core focuses of climate change research (IPCC 2007a). Yet, to date only some 5% of scientific literature discussing climate change mentions uncertainty (**Chapter V**). Uncertainty research is heavily dominated by studies that aim to identify, map and reduce *epistemic uncertainties*

(i.e. uncertainty about facts), especially within natural sciences. Other sources of uncertainty which stem from communication (*linguistic uncertainty*) or human behaviour and values (*human decision uncertainty*) are far more poorly known and addressed (**Chapter V**). Whereas it seems logical that science strives to increase our knowledge about facts, it has been pointed out that in decision-making processes human driven factors, such as motivation, values and beliefs, may far outweigh technical and scientific ones (Morgan and Dowlatabadi 1996; Ascough II et al. 2008). Therefore, instead of asking whether we should or could practice conservation that accounts for climate change, it might be more reasonable to ask whether we would?

There is arguably an urgent need to increase our understanding about the drivers that lead to more efficient conservation implementation (Watson 2005; Knight et al. 2008; **Chapter V**). Different types of uncertainty have so far been very unevenly treated in scientific literature and the separation of disciplines is particularly clear between natural and socio-political sciences (**Chapter V**). Albeit the unknown future development of climate change requires that we continue investigating sources of epistemic uncertainty, it is likely that bridging the research-implementation gap would benefit greatly from studies focusing on linguistic and human decision uncertainties.

4. CONCLUSIONS AND PROSPECTS

In this thesis the different risks and opportunities of proactive conservation planning under climate change were investigated. The major findings from the studies presented in this thesis are that climate change is already rapidly reshaping species distributions (**Chapters II** and **III**) and that ignoring future dynamics can lead to misguided and potentially inefficient conservation decisions (**Chapter III**). The results of this thesis show that modelling future impacts using niche modelling techniques, despite their inherent uncertainties, can provide useful information about how species distributions and conservation statuses will be affected by climate change in the near future (**Chapters II, III** and **IV**, Box 3). Furthermore, they can be used to identify species that are in the risk of disappearing, or that are likely to arrive to a given region as new species (Table 1). Much of the climate change research is currently done on large, often continental-wide scales (**Chapter IV**). Yet, important insights can be obtained when investigating impacts on national scales where the vast majority of conservation decisions are eventually made (**Chapters I, II** and **III**).

Despite recent major improvements, one needs to keep in mind that uncertainty in climate change research is pervasive and cannot ever be entirely eliminated. Nevertheless, the studies in this thesis show that robust solutions both in modelling of future impacts and in spatial conservation prioritizations can be achieved (**Chapters II, III** and **IV**), and that the methodologies presented could be adapted to real-life conservation management. In a rapidly changing world there will always remain scope for improving our understanding about processes and causalities. However, in order to conduct efficient and successful proactive conservation it is likely that the true uncertainties lie elsewhere. As discussed in this thesis, the lack of conservation actions accounting for climate change is not necessarily driven by our lack of knowledge, but our lack of will (**Chapter V**).

An additional message to decision-makers that emerges from this thesis is the importance of nature monitoring. The Earth is currently experiencing its sixth mass extinction (Millennium Ecosystem Assessment 2005), on top of which climate change is rapidly reshaping the patterns of remaining biodiversity. If we want to i) understand ongoing changes, ii) anticipate future impacts, and iii) rapidly react to the threats posed by climate change, comprehensive and accurate information from large-scale surveys and monitoring schemes of biodiversity features is absolutely essential. In particular, species for which predictions of future impacts have higher uncertainty (such as species with already narrow distributions, **Chapters II** and **IV**), intensive monitoring programs might provide the only means of understanding climate change impacts. Research, such as the ones presented in this thesis (**Chapters I, II, III** and **IV**), could not be made without the large biological datasets, the majority of which have been collected with limited resources or purely on voluntary basis. First step for efficient monitoring would be to secure the funding of ongoing atlas projects in a manner that updated data on species distribution changes could be collected in suitable intervals (e.g. 10 years). Second important improvement would be to modify the data collection procedures to include survey effort (**Chapter I**). In addition, national population monitoring schemes

Table 1 | List of bird and herptile species for which climate is expected to become suitable in Finland during 21st century. List shows the Latin, English and Finnish names of those species for which niche models used in **Chapters III** and **IV** predict climatic conditions to become suitable in Finland under all emission scenarios (A1FI, A2, B1 and B2) by the indicated reference year. For further details about modeling techniques see **Chapters III** and **IV**. Note that the models predict only suitability of climatic conditions in a given area. Hence, the ability of the species listed here to migrate to Finland can be further restricted by factors such as dispersal capability, available habitat and interactions with other species.

Reference year: 2050
(Chapter III)

***Aves* – Birds**

Podiceps nigricollis	*Black-necked Grebe*	*Mustakaulauikku*
Ixobrychus minutus	*Little bittern*	*Pikkuhaikara*
Ciconia ciconia	*White stork*	*Kattohaikara*
Ciconia nigra	*Black stork*	*Mustahaikara*
Aythya nyroca	*Ferruginous duck*	*Ruskosotka*
Milvus milvus	*Red kite*	*Isohaarahaukka*
Aquila pomarina	*Lesser spotted eagle*	*Pikkukiljukotka*
Falco cherrug	*Saker falcon*	*Aavikkohaukka*
Tyto alba	*Barn owl*	*Tornipöllö*
Athene noctua	*Little owl*	*Minervanpöllö*
Coracias garrulus	*European roller*	*Sininärhi*
Upupa epops	*Hoopoe*	*Harjalintu*
Picus viridis	*Green woodpecker*	*Vihertikka*
Dendrocopos medius	*Middle spotted woodpecker*	*Tammitikka*
Dendrocopos syriacus	*Syrian woodpecker*	*Syyriantikka*
Galerida cristata	*Crested lark*	*Töyhtökiuru*
Acrocephalus paludicola	*Aquatic warbler*	*Sarakerttunen*
Regulus ignicapillus	*Common firecrest*	*Tulipäähippiäinen*
Ficedula albicollis	*Collared flycather*	*Sepelsieppo*
Parus palustris	*Marsh tit*	*Viitatiainen*
Certhia brachydactyla	*Short-toed treecreeper*	*Etelänpuukiipijä*
Emberiza calandra	*Corn bunting*	*Harmaasirkku*

Reference year: 2080
(Chapter IV)

***Amphibia* – Amphibians**

Salamandra salamandra	*Fire Salamnder*	*Tulisalamanteri*
Bombina bombina	*European Fire-Bellied Toad*	*Kiinankellosammakko*
Pelobates fuscus	*Common Spadefoor Toad*	*Kaivajasammakko*
Pseudepidalea viridis	*European Green Toad*	*Viherkonna*
Epidalea calamita	*Natterjack Toad*	*Haisukonna*
Hyla arborea	*European Tree Frog*	*Euroopanlehtisammakko*
Rana dalmatina	*Agile Frog*	*Hyppysammakko*
Pelophylax ridibundus	*Marsh Frog*	*Mölysammakko*
Rana esculenta	*Edible Frog*	*Vihersammakko*
Rana lessonae	*Pool Frog*	*Lessonansammakko*

***Reptilia* – Reptiles**

Emys orbicularis	*European Pond Turtle*	*Euroopan suokilpikonna*
Lacerta agilis	*Sand Lizard*	*Hietasisilisko*

could be further developed to produce more efficient indicators of climate change impacts by, for example, balancing the representation of different climatic habitats among the surveyed species.

As climate change advances with increasing pace, a critical question for biodiversity persistence is how promptly species will be able to follow their shifting climate envelopes and adapt to new conditions. On a general level, species are clearly responding to changes in their environment (**Chapters II** and **III**) but to exhaustively investigate the drivers that explain mismatches between observed and predicted patterns is beyond the scope of this work. Although these aspects are currently under extensive scrutiny, understanding the evolutionary capacity, ecological traits and interspecific linkages across millions of species is an overwhelming task. An intriguing yet challenging question is how all these factors will influence the structure and composition of future communities. Interesting developments have been made both in community level modelling (e.g. Ferrier and Guisan 2006; Baselga and Araújo 2009; Mokany and Ferrier 2011) as well as by coupling species-specific niche models with mechanistic models (Keith et al. 2008; Kearney and Porter 2009; Morin and Thuiller 2009) to add more precise aspects of species interactions and ecological traits to the predictions. These fields of research are however still in their infancy and our present understanding about the nature of the future communities remains limited.

It is now widely accepted that climate change has put species on the move, but simultaneously observations on species lagging behind their shifting climate envelopes have already been reported (Warren et al. 2001; Devictor et al. 2008; Pöyry et al. 2009; **Chapter II**). It is likely that difficult decisions have to be made about how to deal with species that are not able to follow their climate envelopes, or are in risk of losing their entire suitable climatic space. Aspects such as assisted dispersal (i.e. active transferring of species between their current and future distributions), *ex situ* protection and preservation of genetic heritage, need to be discussed also outside the academia. Given that current GHG emissions are following the most extreme scenario and that species seem to be rapidly responding to the changing climate, we might be forced to make several of these decisions without the adequate scientific knowledge about underlying processes.

This work offers tools to assist in robust decision making when scarce conservation resources need to be allocated under uncertain future conditions. Many of the chapters in this thesis show how knowledge about ongoing changes in biodiversity can be acquired by combining information from several data sources and different modelling methodologies. Furthermore, this thesis provides useful information for conservation practitioners and managers about the ongoing and near future impacts of climate change in Finland that can be utilized, for example, in national conservation strategies and threat assessments.

ACKNOWLEDGEMENTS

This thesis, and the life around it, would have been quite a bit harder and duller without numerous persons to whom I owe my deepest gratitude. I would like to start by thanking the thousands of men and women who have, mostly voluntarily, driven by their passion for nature, spent hours of their free time to reach what sometimes are almost inaccessible terrains, simply to record what sorts of species one might find there 5am in the morning. I cannot thank you enough for the tremendously important work that you do and have done – without your effort and passion the results presented in this thesis could not have been achieved.

On the more personalized part, my greatest gratitude goes to my supervisor Mar Cabeza. Mar, during all these years starting from my master studies, I have never ceased to be amazed by your talent as a researcher. How you so skilfully with just one glimpse subtract the most fascinating and clear messages out from the messy graphs and tables I had brought to you only few minutes earlier. My sincere thank you for pointing me to the right directions when I was struggling to understand my own work, and for being so patient when after all the suggestions and guidance, I still did everything my way. There are not enough words to tell you how much you have inspired me, not just in terms of research, but with your quest to take those tables and figures and make them work in the real world, to reach people and to make a difference. Everything you do, you do with warmth and kindness – kiitos.

I also owe my gratitude to Atte Moilanen who during my years in MRG has been my boss, a mentor and an excellent collaborator. Atte, thank you for everything that you have taught me, and for giving me the opportunity to participate to so many amazing and interesting projects. Your help in these final busy months has been invaluable and I cannot thank you

enough for your tremendous (and successful) PR-work in Australia and New Zealand.

I would like to also sincerely thank Prof. Brian Huntley for finding the time in the middle of the busiest exam period in Durham University to read this work and travel to Helsinki to be my opponent. I am equally thankful to my pre-examiners Prof. Janne Kotiaho and Prof. Mikko Mönkkönen for their swift and rigorous work in evaluating the earlier version of this thesis, and for their excellent comments that improved it. Mikko has also been a member of my thesis advisory committee together with Dr. Hannu Pietiäinen and I have been very grateful for having two such prominent persons in my committee. Those yearly meetings provided a good opportunity to stop and think where this work was heading at.

I have several co-authors who all have contributed to this thesis in many ways, and I feel very privileged for having had the opportunity to work with such great minds. I would like to particularly thank Miguel Araújo and Wilfried Thuiller who so kindly hosted my visits to Madrid and Grenoble. Our projects have taught me a lot, and I would like to thank you for your collaboration, your guidance and inspiration.

I feel extremely lucky for having had the opportunity to do my PhD in the best research group one could ever imagine. Dear MRG, you set the bar high for any future working surroundings and I will greatly miss our inspiring, amazing and friendly lab with all the seminars, coffee breaks, annual meetings and end of summer parties. And Pgi talks! Ilkka, my academic grand-grandfather, thank you for bringing together this wonderful group of people, for being such an inspiring and amazing group leader and a role model. A big special thank you to Luisa for taking care of me during my very first year in MRG, for being such an amazing friend; to my fantastic office roommates now and in the past: Jenni, Veera, Hanna, Aija and Johanna K.; to Itsuro, Jarno, Andreia, Maaike and Eli for all the fun, good food and music, your friendship has made my life so much richer; to Tanjona for the fun tee breaks, the Big Bang Theory and 'shared' banana chips; to Otso for tolerating my never-ending secondary school level stats questions; to Marjo for being such amazing friend and a mentor with everything during these last months, this would not have happened without you!; a big HURRAA to Anne and Anniina, my best ever cheerleaders – your support made it all happen; to Evgeniy, for always being there when I was getting desperate with GIS; to Sami and Viia (and also Camilla, Tuuli and Marika) for being there when I was getting even more desperate with computers and bureaucracy (I never learned how to fill those holiday forms correctly); to Sami again, for no-one would be reading this book if it wasn't for you.

I am also very grateful to the many staff members who are the true reason that our department and faculty is up and running. A special thank you to the wonderful and skilled LUOVA coordinators, Anna-Liisa, Jonna and Anni, who are taking such great care of us PhD students and putting so much effort in providing the best possible education and working surroundings.

Fridays are great days, but they were made even better by our fantastic Journal (Pulla) Club with its internal and external members. Astrid, Anni, Joona, Johanna, Laura, Maria, Laure, Silvija, Henna, Ninni, Andrea, Daniel, Saija, Ricardo, Raquel and many other short- and long-term visitors, many thanks for the inspiring discussions, for sharing the sometimes substantial agony of doing good science or agreeing on a time for next meeting. And just simply for the fun of trashing, and the great Pulla. Many of you helped me so much in proof reading this thesis, especially Anni who is among the few persons who have actually read it all. I owe you my deepest gratitude. A big special thank you also to Maria and Laure, my dear friends who made my stays in Madrid and Grenoble so wonderful.

For so many years, the light of my weekly PhD life has been the Viikki Lunch Society. Antti, Joona, Pekka, Mari, Maiju, Essi, Marco, Heini and Nica, thank you my dear friends for making me to take a break from my work every day, for such fun lunch times, the peer support, the zombies, the movies and just everything. There are and have been so many wonderful people at our department, all of which I am grateful to have become friends with and who have been such excellent peers: Vilppu, Jenni, Tuomas, Eddie, Johan, Kim, Aleksi, Mike, Maria D. and Celine, thank you for the fun times and your friendship. Christoph, you have been my best Swiss peer and friend. Kiitos kaikista hauskoista hetkistä, varsinkin rapujuhlissa. Chris, thank you for the dances and the crazy karaoke. Jostein, I have quickly learned how much I miss our discussions (where you question the existence of anything and everything), the fussball and the flag on the marble arch. Takk for din vennskap Mister J*. Katja, from Viikki to Slovakia (or was it Slovenia?) you have been an awesome friend and a mentor, both in science and life, tack so mycket för allt min kära vän. And finally, Joona, the best peer and Zonation co-advocate. This is the

third time I mention you in my acknowledgements, which just goes to show how much great time, both workwise and lifewise, I have had with you. Thank you for your friendship and support, and sorry for always dragging you to the after parties (totally against your will) 4am in the morning.

During times when working was the last thing in my mind, my life has been blessed with my dear friends outside the academia. Noora, Mervi, Pippa and Elina, I owe you special thanks for being in my life. We have shared so many special moments and it has been an honour to grow up with you, becoming the person who I am. And my lovely girls, Minttu, Hanna, Laura N., Laura L., Meri, Sanna K., Sanna M., Karoliina, Suvi, Eeva and Reetta, there are no words to say how much your friendship means to me. Thank you for being there for me, for all the fun times in Finland and abroad, above and under water, for your love and your support.

There have been many lucky moments in my life, the first of which was when I was born into an amazing family. Or a clan, as it might also be called. Kauppi, Arni, Jenni and Vassi, thank you for being such great siblings, for looking over me, for all the car trips to our summer cabin(s), for the fights over the last pancake, for tolerating my moods, and for being the magnificent and beautiful persons you are. I know for certain that my life would be so much duller without your company, and feel grateful to know that you will always be in my life. Also Jenni, Saija, Arve and Leena, my wonderful sister- and brother-in-laws, thank you for your support and friendship throughout these years. Nine (so far) little stars have brightened my life during the past ten years: Oiva, Aksel, Ella, Lina, Iida, Henri, Teo, Valle and Enni, thank you for bringing so much joy and happiness in our lives. Finally, I would like thank my Mum, who is the very reason I ever became a biologist. You are the one who taught me to love and respect nature, and still today you are the one of us who identifies the plants, mushrooms and animals with better accuracy. Kiitos kaikesta rakkaudesta ja tuesta, yhteisistä hetkistä, sieni- ja marjaretkistä, ihanista mekoista ja mahtavista matkoista maan ääriin.

This work has been funded by LUOVA Graduate School, Maij and Tor Nessling Foundation, Finnish Cultural Foundation and EU 7th Framework Project RESPONSES.

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